

DIURNAL AND NOCTURNAL BEHAVIOR OF BREEDING AMERICAN AVOCETS

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ABSTRACT.—We studied nocturnal and diurnal behavior of breeding American Avocets (*Recurvirostra americana*) at the Jay Dow, Sr. Wetlands in the northwestern Great Basin, USA. Seven-day observation periods were centered on two full moons when ambient light was maximal and auxiliary lighting unnecessary. We recorded avocet density, habitat use, interbird distances, and behavior three times daily (beginning at 07:00, 15:00, 23:00 PST) for 14 days. We calculated the mean proportion of individuals within flocks engaged in four behavior classes (foraging, copulating, agonistic, other). Foraging birds were further subdivided by technique (pecking, dunking, scything). Avocets copulated with similar frequencies during the morning, afternoon, and night. Avocets were more aggressive and closely spaced at night than during day. The full repertoire of behaviors seen during daylight also occurred at night, though frequencies of particular behaviors, flock location, and interbird distances varied among morning, afternoon, and nighttime observations. The role of nocturnal reproductive behavior should be assessed in species generally perceived as being diurnal. Received 12 January 2003, accepted 20 March 2003.

Nocturnal foraging throughout the annual cycle is common among coastal shorebirds in North and South America, Africa, and Europe (Goss-Custard 1969, McNeil and Robert 1988, Zwarts et al. 1990, McNeil 1991, Evans and Harris 1994, Staine and Burger 1994), yet there is relatively little understanding of the latitudinal and seasonal variation in nocturnal behavior within and among shorebird species. Researchers have proposed that tactile foragers should be relatively less affected by darkness than visual foragers (Vader 1964, Goss-Custard 1969, Evans 1976, Dugan 1981), yet plovers (Charadriidae) are primarily visual foragers that commonly forage at night (Pienkowski 1983). The relatively large eye in relation to head size of plovers may enhance visual detection of prey (Evans 1976), yet several smaller-eyed sandpipers (Scolopacidae) also forage visually at night, including Common Redshanks (*Tringa totanus*; Goss-Custard 1969), Semipalmated Sandpipers (*Calidris pusilla*; Evans 1979), and Whimbrels (*Numenius phaeopus*; McNeil and Rompré 1995). Nocturnal bird species are morpholog-

ically and physiologically adapted to nocturnal activity as their eyes contain a higher proportion of rods in the retina compared to diurnal species, and retinal sensitivity is higher among birds that forage visually at night compared to those that use tactile techniques (Tansley and Erichsen 1985; Rojas De Azuaje et al. 1993; Rojas et al. 1999a, 1999b; McNeil et al. 1999).

Although several studies have examined nocturnal foraging at coastal locations, there are few studies of shorebird nocturnal behavior on the breeding grounds and at inland locations. During the breeding season, Red-wattled Lapwings (*Vanellus indicus*) and Stone-curlews (*Burhinus oedipnemus*) are vocal primarily at night (Bannerman 1959), and some species display or call from dusk into the night (*Scolopax* spp.: Sheldon 1961, Krohn 1971, Stribling and Doerr 1985; *Gallinago* spp.: Lemnell 1978). Breeding Common Ringed Plovers (*Charadrius hiaticula*), and Piping Plovers (*C. melodus*) forage at night (Pienkowski 1983, Staine and Burger 1994), and the role each sex plays in nocturnal incubation also has been examined for several species (Laven 1940, Mundahl 1982, Warriner et al. 1986, Staine and Burger 1994, Thibault and McNeil 1995a, Warnock and Oring 1996). American (*Recurvirostra americana*) and Pied avocets (*R. avosetta*) forage diurnally and nocturnally throughout the annual cycle (Evans and Harris 1994, Dodd and Colwell 1996, Hötter 1999, Johnson et al. 2002), and

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TABLE 1. Akaike Information Criteria (AIC) for candidate models used to examine variation in American Avocet behavior during the daily cycle at Jay Dow, Sr. Wetlands, Lassen County, California, 2001.

Model ^a	Number of parameters	ΔAIC^b	AIC weight ^c
Overall behavior			
{T, L, D, W, L \times D}	5	0.0	0.865
{T, L, D, W, T \times L, T \times D, L \times D}	7	3.7	0.135
{T, FS, L, D, EL, W, S, I, dist, inter}	23	35.1	<0.001
Habitat use			
{T, L, FS, A, T \times L}	5	0.0	0.932
{T, FS, L, F, A, T \times FS, T \times L}	8	5.9	0.050
{T, FS, L, F, A, S, T \times FS, T \times L, FS \times L}	9	7.8	0.019
Interbird distance			
{T, FS, L, D, EL, T \times L, L \times D}	7	0.0	0.999
{T, FS, L, D, EL, inter}	15	15.2	0.001
{T, FS, L, D, EL, M, A, C, F, W, S, I, inter}	22	29.0	<0.001
Foraging technique			
{T, FS, L, D, EL, W, I, T \times EL, L \times D}	9	0.0	0.873
{T, FS, L, D, EL, W, I, T \times EL, L \times D, T \times D, FS \times L}	11	3.9	0.127
{T, FS, L, D, EL, W, I, inter}	17	15.5	<0.001

^a T = treatment (morning = 07:00, afternoon = 13:00, night = 23:00), FS = flock size, L = location, D = date, EL = early/late season, F = proportion foraging, M = proportion self maintenance, C = proportion copulating, A = proportion agonistic, W = proportion in open water, S = proportion on shore, I = proportion on islands, I = proportion of birds <1 m apart, S = proportion of birds 1–5 m apart, dist = all interbird distance classes (<1, 1–5, 6–10, 11–20, >20 m), inter = all two-way interactions.

^b ΔAIC is the rank of each model by rescaling the model with a minimum AIC value to zero ($\Delta AIC = AIC_i - AIC_{min}$).

^c AIC weights are the likelihood of the model given the data (Akaike weights).

several shorebird species, including the American Avocet, copulate at night (Johnson et al. 2002).

Knowledge of nocturnal behavior is essential for understanding both ecology and energetics, yet current understanding of shorebird nocturnal behavior is limited. Shorebird habitat use and foraging technique varies during the daily cycle (Rompré and McNeil 1995, Robert et al. 1989). Nocturnality also appears to affect energy balance (Pienkowski 1983) and, potentially, reproductive strategy (Johnson et al. 2002). Recent technological advances in night vision equipment facilitate the study of nocturnal behavior, permitting a more thorough approach to behavioral ecology and allowing more accurate assessment of energy budgets, space use, and social interactions. The aim of this study was to describe the extent of nocturnality among American Avocets breeding at an inland location.

METHODS

Study area.—We studied American Avocet behavior at the Jay Dow, Sr. Wetlands (JDW; 40° 07' N, 120° 14' W, elevation 1,220 m).

JDW is a 540-ha constructed wetland containing 16 bodies of water at the southern end of Honey Lake, Lassen County, California. JDW includes a seep draining to Honey Lake, a natural playa lake, and 14 constructed ponds. With the exception of the seep, water was maintained at a constant level from March to July. Honey Lake Basin (23,000 ha) is characterized by agricultural production and by Great Basin desert scrub vegetation on gently sloping to nearly level alluvial fans, floodplain, and basin floor. Common vegetation at JDW included sagebrush (*Artemisia tridentata*), saltbrush (*Atriplex spinosa*), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus* spp.), saltgrass (*Distichlis spicata*), rush (*Juncus* spp.), and cattail (*Typha latifolia*). Avocets arrive at JDW during late March and initiate clutches from the end of April through the beginning of June (Robinson and Oring 1997).

Observations.—During 2001, we centered 7-day observation periods on two full moons (3–10 May and 2–8 June) when ambient light was maximal and auxiliary lighting unnecessary. We used a hand-held generation III night

TABLE 2. Multivariate analysis of variance for time of day (07:00, 13:00, 23:00) and covariate effects on American Avocet behavior at Jay Dow, Sr. Wetlands, Lassen County, California, 2001.

Factor	Degrees of freedom		Wilk's lambda	<i>F</i>	<i>P</i>
	Numerator	Denominator			
Overall behavior					
Time of day	8	210.00	0.278	23.52	<0.001
Date	4	105.00	0.679	12.40	<0.001
Location	28	380.01	0.434	3.54	<0.001
Proportion birds in open water	4	105.00	0.770	7.84	<0.001
Date × location	24	367.51	0.663	1.92	0.007
Habitat use					
Time of day	6	200.00	0.691	6.77	<0.001
Location	21	287.70	0.199	10.37	<0.001
Flock size	3	100.00	0.934	1.62	0.189
Proportion birds agonistic	3	100.00	0.954	1.61	0.192
Time of day × location	36	296.19	0.568	1.73	0.008
Interbird distance					
Time of day	10	182.00	0.328	13.59	<0.001
Date	5	91.00	0.719	7.12	<0.001
Month	5	91.00	0.744	6.25	<0.001
Location	35	385.23	0.630	1.28	0.139
Flock size	5	91.00	0.728	6.79	<0.001
Location × time of day	60	429.90	0.644	0.70	0.952
Location × date	30	366.00	0.570	1.84	0.005
Foraging technique					
Time of day	6	202.00	0.749	5.24	<0.001
Date	3	101.00	0.799	8.47	<0.001
Month	3	101.00	0.789	8.98	<0.001
Location	21	290.57	0.430	4.73	<0.001
Flock size	3	101.00	0.891	4.14	0.008
Proportion birds in open water	3	101.00	0.645	18.54	<0.001
Proportion birds <1 m apart	3	101.00	0.892	4.10	0.009
Time of day × month	6	202.00	0.865	2.54	0.022
Location × date	18	286.16	0.717	1.98	0.011

vision scope with a 100-mm zoom lens (NiteMate NAV-3, Litton) to observe avocet behavior at night. We established 43 observation points that enabled total coverage of JDW during diurnal and nocturnal surveys. We recorded avocet density, habitat use, and behavior three times daily (morning, afternoon, and night: 07:00, 15:00, and 23:00 PST, respectively) for 14 days at each observation point. We recorded avocet density for each pond and the entire study site. We recorded the distance from each individual to the nearest next individual as one of five interbird distance classes (<1 m, 1–5 m, 6–10 m, 11–20 m, >20 m), and we categorized occupied habitats as shoreline, open water, or island. We categorized behavior as foraging, copulating, agonistic, or other. Agonistic behavior refers

to intraspecific encounters, and behavior class “other” included self maintenance, nest building, and incubation. We further subdivided foraging birds by technique (pecking, dunking, scything). Foraging classes corresponded to the visual (pecking) and tactile (dabbling scythe and multiple scythe) foraging techniques described by Hamilton (1975). After we completed each survey of JDW (approximately 1 h), we returned to the three locations containing the largest avocet flocks and scanned flocks, recording each bird's behavior. We scanned each flock five times with ≥ 3 min between successive samples. Time required per scan sample (1–3 min) varied with flock size. The five scans represented subsamples of each flock, which we used as our experimental unit (mean proportion of total number of av-

ocets present at JDW for which individual behavior was recorded after each census was 0.74 ± 0.07 SD, $n = 42$ censuses, $n = 126$ flocks).

Analysis.—From each set of scans, we calculated the mean proportion of individuals within each flock engaged in the four behavior classes, as well as the proportion of foraging birds utilizing each foraging technique. We also calculated the proportion of birds in each habitat, and the proportion of birds in each of five interbird distance classes. These methods produced four multidimensional response vectors for the behavior of each flock. The response vectors (behavior, foraging technique, habitat use, interbird distance) served as independent data points for analysis. Because percentages within vectors summed to 100 and were thus correlated, it was necessary to use multivariate analysis techniques. We arc-sine transformed data and set $\alpha = 0.05$ *a priori*, then tested for behavioral variation during the daily cycle using a multivariate analysis of covariance model (MANCOVA) for each response vector, with time of day (morning, afternoon, night) as the main effect and month (May, June), date (day one through seven during May and June sampling periods), location (pond), and flock size as covariates (Seber 1984, Johnson and Wichern 1988). Behavioral responses not modeled by the response vector also were included as covariates in each model. We compared potential models for each behavioral response beginning with the saturated two-way interactive model using information-theoretic methods to direct model selection (Burnham and Anderson 1998). For each model we calculated Akaike information criteria (AIC), which were used to compare candidate models to achieve the most parsimonious model that accurately represented the data (Burnham and Anderson 1998, Anderson et al. 2000).

We used three-way ANOVA to examine avocet density at ponds during the daily cycle (morning, afternoon, night) and throughout the study (May, June). We used SAS macro FXQLQLQL (Fernandez 1999) to check normality and equal variance assumptions of ANOVA and examined student residuals for the presence of significant outliers and influential observations. Data differed significantly from normality and variances were not equally dis-

tributed. When we performed Huber's iterative robust ANOVA to reduce the impact of highly influential observations, the data assumed a normal distribution (D'Agostino-Pearson Omnibus $P = 0.62$; Huber 1981). We used Tukey's test for comparison of all means, and we report nontransformed values.

RESULTS

Avocet behavior varied within the daily cycle, and among days, locations, and months. The mean number of avocets was similar at all times of day (morning: 148 ± 14 SE, afternoon: 145 ± 12 SE, night: 157 ± 8 SE; $P = 0.92$), but more avocets were present early in the breeding season than later (May: 170 ± 6 SE, June: 130 ± 10 SE; $P = 0.015$).

Behavior.—Behavior (foraging, copulating, agonistic, other) varied as a function of time of day, date, proportion of birds in open water habitat, and location (Tables 1, 2). There also was a significant interaction between date and location (Tables 1, 2). We found no significant difference in the proportion of avocets copulating or foraging throughout the day (Table 3). However, birds were five times more agonistic at night compared to morning and afternoon (Table 3), and birds engaged in other behavior less at night than during morning and afternoon (Table 3).

Foraging technique.—Foraging technique varied as a function of time of day, flock size, location, date, month (Table 4), open water habitat, and proportion of birds < 1 m from another avocet (Tables 1, 2). There also was an interaction between time of day and month and between location and date (Tables 1, 2). Avocets foraged by pecking more in the morning compared to afternoon and night (Table 3). The proportion of birds dunking increased from morning to afternoon and again from afternoon to night (Table 3), and higher proportions of avocets foraged by dunking early in the breeding season compared to later (Table 4). Avocets scythed less at night than during day (Table 3), and lower proportions of avocets used the scythe technique to forage early in the breeding season than later (Table 4).

Habitat use.—Habitat use by avocets varied as a function of time of day and location, and there was a significant interaction between these two variables (Tables 1, 2). Avocets fre-

TABLE 3. Mean (\pm SE) proportion of American Avocets conducting various behaviors in different habitats during three daily sampling periods (morning = 07:00, afternoon = 13:00, night = 23:00) in early (May; n = 21 flocks) and late (June; n = 21 flocks) breeding season and combined (May–June; n = 42) at Jay Dow, Sr. Wetlands, Lassen County, California, 2001. Different superscripts within a row denotes statistically different means (Tukey’s test, $P < 0.05$).

	Morning			Afternoon	
	May	June	May–June	May	June
Behavior					
Agonistic	0.019 \pm 0.007	0.026 \pm 0.009	0.023 \pm 0.006 ^A	0.040 \pm 0.009	0.033 \pm 0.008
Copulate	0.017 \pm 0.005	0.005 \pm 0.002	0.011 \pm 0.003 ^A	0.027 \pm 0.005	0.002 \pm 0.001
Other	0.449 \pm 0.060	0.350 \pm 0.033	0.400 \pm 0.035 ^A	0.421 \pm 0.042	0.425 \pm 0.035
Foraging	0.515 \pm 0.057	0.620 \pm 0.034	0.567 \pm 0.034 ^A	0.512 \pm 0.038	0.540 \pm 0.033
Dunking	0.591 \pm 0.075	0.466 \pm 0.063	0.529 \pm 0.049 ^A	0.777 \pm 0.056	0.446 \pm 0.068
Pecking	0.395 \pm 0.077	0.213 \pm 0.047	0.304 \pm 0.047 ^A	0.186 \pm 0.053	0.231 \pm 0.040
Scything	0.014 \pm 0.005	0.321 \pm 0.058	0.168 \pm 0.037 ^A	0.037 \pm 0.027	0.323 \pm 0.063
Habitat					
Water	0.510 \pm 0.081	0.847 \pm 0.038	0.679 \pm 0.051 ^A	0.705 \pm 0.054	0.733 \pm 0.038
Island	0.261 \pm 0.073	0.042 \pm 0.020	0.151 \pm 0.041 ^A	0.130 \pm 0.050	0.039 \pm 0.019
Shore	0.229 \pm 0.053	0.111 \pm 0.028	0.170 \pm 0.031 ^A	0.164 \pm 0.027	0.227 \pm 0.033
Interbird distance					
<1 m	0.160 \pm 0.032	0.062 \pm 0.016	0.111 \pm 0.020 ^A	0.222 \pm 0.032	0.113 \pm 0.024
1–5 m	0.230 \pm 0.029	0.180 \pm 0.025	0.205 \pm 0.019 ^A	0.280 \pm 0.021	0.243 \pm 0.027
6–10 m	0.209 \pm 0.024	0.221 \pm 0.024	0.215 \pm 0.017 ^A	0.175 \pm 0.025	0.184 \pm 0.024
11–20 m	0.193 \pm 0.031	0.380 \pm 0.036	0.287 \pm 0.028 ^A	0.144 \pm 0.018	0.292 \pm 0.045
>20 m	0.207 \pm 0.029	0.157 \pm 0.025	0.182 \pm 0.019 ^A	0.179 \pm 0.016	0.169 \pm 0.027

quented certain ponds at specific times of the day and some ponds were used predominately during either the early or late portion of the breeding season (Fig. 1; ANOVA: $F_{46,416} = 36.39$, $P < 0.0001$; location $F_{10,416} = 61.65$, $P < 0.0001$; month $F_{1,416} = 13.44$, $P = 0.0003$; time of day $F_{2,416} = 0.49$, $P = 0.61$; time of day \times location $F_{20,416} = 0.347$, $P < 0.0001$; month \times location $F_{10,416} = 17.84$, $P < 0.0001$; month \times time of day $F_{2,416} = 9.0$, $P = 0.0001$). Island habitat use decreased from morning through night (Table 3), and a greater proportion of avocets used islands early in the breeding season compared to later (Table 4). Mean proportion of avocets utilizing open water did not differ significantly among the three sampling periods (Table 3), but avocets used open water more often late in the breeding season (Table 4). The proportion of avocets utilizing shoreline habitat did not differ significantly among the three daily sampling periods (Table 3) or between early and late season (Table 4).

Interbird distance.—Interbird distance varied as a function of time of day, flock size, date, and month (Tables 1, 2). There also was

an interaction between date and location (Tables 1, 2). Mean proportion of avocets < 1m apart was higher at night than during day (Table 3). Similarly, the proportion of birds 1–5 m apart was higher in the afternoon compared to morning but greatest at night (Table 3). The proportion of birds in all larger interbird distance classes was least at night (Table 3). Mean proportion of avocets < 1m apart was higher early in the season, and a larger proportion of birds were spaced farther apart later in the season (Table 4).

DISCUSSION

All behaviors performed by breeding American Avocets during the day also occurred at night, though frequencies of particular behaviors, flock location, and interbird distances varied among morning, afternoon, and night. Nocturnal social behavior was sufficiently frequent that further study of avocet behavior must consider nocturnal habits. While observations in this study were limited to the week around the full moon, earlier observations at the study site confirm that several shorebird species are socially active at

TABLE 3. Extended.

Afternoon	Night		
May–June	May	June	May–June
0.036 ± 0.006 ^A	0.186 ± 0.017	0.210 ± 0.021	0.198 ± 0.014 ^B
0.014 ± 0.003 ^A	0.025 ± 0.008	0.008 ± 0.003	0.016 ± 0.004 ^A
0.423 ± 0.027 ^A	0.240 ± 0.028	0.160 ± 0.019	0.200 ± 0.018 ^B
0.526 ± 0.025 ^A	0.549 ± 0.027	0.623 ± 0.026	0.586 ± 0.019 ^A
0.612 ± 0.051 ^B	0.816 ± 0.037	0.685 ± 0.055	0.750 ± 0.034 ^C
0.209 ± 0.033 ^B	0.142 ± 0.032	0.204 ± 0.045	0.173 ± 0.028 ^B
0.180 ± 0.041 ^A	0.042 ± 0.017	0.111 ± 0.028	0.076 ± 0.017 ^B
0.719 ± 0.033 ^A	0.776 ± 0.035	0.768 ± 0.027	0.772 ± 0.022 ^A
0.085 ± 0.027 ^B	0.053 ± 0.016	0.002 ± 0.001	0.027 ± 0.009 ^C
0.196 ± 0.022 ^A	0.171 ± 0.029	0.231 ± 0.027	0.201 ± 0.020 ^A
0.167 ± 0.021 ^A	0.438 ± 0.024	0.305 ± 0.023	0.372 ± 0.019 ^B
0.261 ± 0.017 ^B	0.312 ± 0.017	0.419 ± 0.016	0.365 ± 0.014 ^C
0.179 ± 0.017 ^A	0.063 ± 0.009	0.138 ± 0.010	0.101 ± 0.009 ^B
0.218 ± 0.027 ^B	0.086 ± 0.010	0.079 ± 0.015	0.082 ± 0.009 ^C
0.174 ± 0.015 ^A	0.101 ± 0.012	0.059 ± 0.010	0.080 ± 0.008 ^B

night throughout the lunar cycle (Johnson et al. 2002). Further, Pied Avocets are active at night, regardless of lunar illumination (Hötter 1999).

Copulations.—Nocturnal copulation rarely has been reported, but is not necessarily uncommon among shorebirds (Lemnell 1978, Johnson et al. 2002). We found avocets copulating with similar frequency during morning, afternoon, and night, and previous observation at JDW found several shorebird species, including avocets, copulating at night regardless of lunar phase (Johnson et al. 2002). Theory on mating strategy has failed to address the possibility of nocturnal reproductive tactics among most shorebirds (e.g., Oring 1982). Considering that Ring-billed Gull (*Larus delawarensis*) copulations are interrupted less often at night (Hébert and McNeil 1999), and our observation that nocturnal copulations are likely to play substantial roles in avocet reproduction, study of shorebird nocturnality is critical for accurate assessment of reproductive tactics among temperate breeding shorebirds.

Interbird distance and agonistic behav-

ior.—Avocets were more aggressive and more closely spaced at night than during the day, and the mean proportion of agonistic birds was five times higher at night. Avocets apparently increased nocturnal agonistic behavior at the expense of self maintenance or incubation, as the proportion of birds engaged in other behaviors was 50% less at night. Avocets and other shorebirds potentially are better able to reduce incubation duties at night when the risk of desiccation to uncovered eggs due to overheating is minimal (Thibault and McNeil 1995a). Shorebird eggs are robust to cool temperatures, but highly susceptible to extreme heat. Thus, avocets may be more prone to leave the nest at night when ambient temperature is low. Conversely, it is possible that we failed to detect incubating birds during nocturnal observations. However, this is not likely as there was no significant difference in the number of birds observed on the entire wetland during morning, afternoon, and nocturnal surveys.

Avocets also may be tightly spaced at night to reduce the threat of predation. However, nocturnal agonistic encounters generally were

TABLE 4. Mean (\pm SE) proportion of American Avocets performing various behaviors in different habitats early (May; $n = 63$ flocks) and late (June; $n = 63$ flocks) in the breeding season at Jay Dow, Sr. Wetlands, Lassen County, California, 2001. Different superscripts within a row denotes statistically different means (Tukey's test, $P < 0.05$).

	May	June
Behavior		
Agonistic	0.082 \pm 0.012 ^A	0.089 \pm 0.013 ^A
Copulate	0.023 \pm 0.004 ^A	0.005 \pm 0.001 ^A
Other	0.370 \pm 0.028 ^A	0.312 \pm 0.022 ^A
Foraging	0.526 \pm 0.024 ^A	0.594 \pm 0.018 ^A
Dunking	0.728 \pm 0.035 ^A	0.532 \pm 0.038 ^B
Pecking	0.241 \pm 0.035 ^A	0.216 \pm 0.025 ^A
Scything	0.031 \pm 0.011 ^A	0.252 \pm 0.032 ^B
Habitat use		
Water	0.664 \pm 0.037 ^A	0.783 \pm 0.021 ^B
Island	0.148 \pm 0.031 ^A	0.027 \pm 0.009 ^B
Shore	0.188 \pm 0.022 ^A	0.190 \pm 0.018 ^A
Interbird distance		
<1 m	0.273 \pm 0.023 ^A	0.160 \pm 0.018 ^B
1–5 m	0.274 \pm 0.014 ^A	0.281 \pm 0.018 ^A
6–10 m	0.149 \pm 0.014 ^A	0.181 \pm 0.012 ^A
11–20 m	0.141 \pm 0.014 ^A	0.250 \pm 0.025 ^B
>20 m	0.163 \pm 0.013 ^A	0.128 \pm 0.014 ^B

loud and created a commotion easily detected by predators. Hawk and owl predation is a key factor in shorebird mortality during the non-breeding season (Page and Whitacre 1975, Townshend 1984, Whitfield 1985, Whitfield et al. 1988); however, the extent of diurnal versus nocturnal raptor predation on shorebirds, especially during the breeding season, has not been thoroughly investigated (Townshend 1984).

Foraging.—The proportion of birds engaged in foraging behavior varied from 0.50–0.60 throughout the daily cycle and the entire season; however, foraging technique was less consistent. Change in prey visibility or availability may account for daily and seasonal variation in foraging technique. A shift to tactile foraging techniques at night may be more efficient for avocets if prey is difficult to detect visually at lower light intensities. Eurasian Oystercatchers (*Haematopus ostralegus*), yellowlegs (*Tringa flavipes*, *T. melanoleuca*), Black-winged Stilts (*Himantopus himantopus*), and Willets (*Catoptrophorus semipalmatus*) showed less visual foraging and more tactile foraging at night (Hulscher

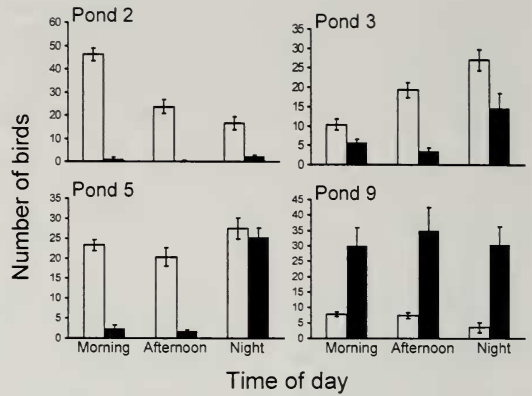


FIG. 1. Variation in mean number of American Avocets at four locations at Jay Dow, Sr. Wetlands, Lassen County, California during morning (07:00), afternoon (15:00), and night (23:00) observations, 2001. White bars represent May observations ($n = 7$), black bars represent June observations ($n = 7$), and error bars provide standard error (ANOVA: all locations, $n = 11$; $F_{46,416} = 36.39$, $P < 0.0001$; location $F_{10,416} = 61.65$, $P < 0.0001$; month $F_{1,416} = 13.44$, $P = 0.0003$; time of day $F_{2,416} = 0.49$, $P = 0.61$; time of day \times location $F_{20,416} = 0.347$, $P < 0.0001$; month \times location $F_{10,416} = 17.84$, $P < 0.0001$; month \times time of day $F_{2,416} = 9.0$, $P = 0.0001$).

1974, 1976; Evans 1976; McNeil and Robert 1988; Robert and McNeil 1989, McNeil and Rompré 1995, Rompré and McNeil 1995). Eye morphology and physiology are correlated with nocturnal foraging behavior in many bird species (Rojas De Azuaje et al. 1993; Rojas et al. 1999a, 1999b; McNeil et al. 1999). Shorebirds that used tactile foraging techniques, including Short-billed Dowitchers (*Limnodromus griseus*), American Woodcocks (*Scolopax minor*), and Willets exhibited lower retinal sensitivity and had lower rod:cone ratios compared to those that used visual foraging techniques at night, such as Black-winged Stilts and Wilson's Plovers (*Charadrius wilsonia*; Rojas et al. 1999a, 1999b). Variation in foraging technique between day and night also may be a consequence of variation in prey behavior during the daily cycle, resulting in changes in prey availability. Similar or distinct prey communities may be available to shorebirds in common or discrete habitats between day and night (Thibault and McNeil 1995b, Rompré and McNeil 1995). Overall, shorebird prey were more abundant at night at a Venezuelan lagoon (McNeil et al. 1995), and

two annelid prey species commonly taken by shorebirds in Europe (*Nereis diversicolor*, *Lumbricus terrestris*) also were most available at night (MacLennan 1979, Dugan 1981).

Habitat use.—Although some ponds at JDW were used consistently throughout the daily cycle and the entire breeding season, avocets frequented certain ponds at specific times of the day and some ponds were used predominately during either the early or late portion of the breeding season. Variation in prey community distribution and composition during both the daily and breeding cycle may affect avocet distribution. Habitat use also varied within ponds at JDW as birds were found less often on islands and more often in open water late in the breeding season. Reduced use of islands may be a consequence of nest loss. Avocets commonly nest on islands at JDW, and if early season island nesters lost clutches and failed to reneest, we would expect use to shift from islands (incubation) to either shore or open water.

American Avocets, and potentially other waterbirds, do not fit the typical diurnal, nocturnal, or crepuscular paradigm. Rather, avocets practice a labile life history strategy throughout the annual cycle (Evans and Harris 1994, Dodd and Colwell 1996, Hötter 1999, Johnson et al. 2002). Such behavioral plasticity enables birds to profit in the dynamic environments they commonly inhabit. At coastal locations, a labile foraging strategy independent of solar cycle allows avocets to take advantage of tidally induced changes in resource availability (Robert et al. 1989). Further, avocet energy acquisition appears independent of day length, which also may be beneficial to avocets breeding in arid environments. Nocturnal sexual and agonistic behaviors in avocets are sufficiently frequent that further study of avocet reproductive behavior must consider nocturnal habits. The role of nocturnal reproductive behavior should be assessed in species generally perceived as being diurnal.

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